Popular Agriculture 2(4) 103-109(July, 2026)
Published at popularagriculture.com

Global E-Magazine
ISSN: 3139-7603

POPULAR ARTICLE

Securing the harvest: Leveraging breeding innovations for developing drought-resilient

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Manuscript received: June 12, 2026; Decision on manuscript, June 30, 2026; Manuscript accepted: July 14, 2026

Introduction and intricacies of the subject

Climate change and the resulting rise in drought severity pose a growing threat to global crop productivity, with staple cereal yields already declining and rainfed systems such as India's bearing a disproportionate burden. Water deficit disrupts plant function at every level, impairing photosynthesis, damaging reproductive development and triggering oxidative stress, ultimately eroding yield and quality. Addressing this challenge requires integrating multiple breeding strategies rather than depending on any single approach. Conventional breeding, though foundational, remains slow due to its reliance on multi-year phenotypic evaluation. Pre-breeding complements this by introgressing tolerance genes from crop wild relatives into elite backgrounds, expanding the genetic base available to breeders. Molecular approaches, including marker-assisted backcrossing, recurrent selection and genomic selection, enable faster, genotype-level selection independent of crop maturity. Transgenic and gene-editing technologies extend these gains further, introducing targeted stress-responsive genes such as DREB1A, NAC transcription factors, and HVA1 across species barriers. This review consolidates trait mechanisms, wild genetic resources, candidate genes, and released varieties relevant to drought tolerance, underscoring the need for coordinated investment across this breeding continuum to secure future food supplies.

Introduction

Climate change presents an existential threat to global agricultural sustainability, with rising temperatures and severe water deficits posing critical risks to crop productivity. According to the Stanford-led study, global yields of major staples such as barley, maize and wheat have already declined by 4% to 13% relative to baseline climatic conditions. India’s agriculture is exceptionally vulnerable to these shifts due to its vast reliance on monsoon precipitation and extensive rainfed cultivated lands. In India, between 2016-17 to 2021-22, drought conditions caused severe damage, resulting in ~33% yield loss across ~35 million hectares of cropped area. These escalating environmental pressures underscore the imperative need to develop climate-resilient crop varieties to safeguard future national and global food security. Behind these yield and grain-filling stages. Drought impairs chlorophyll synthesis and photosystem function and induce stomatal closure, which restricts CO2 diffusion into leaves, thereby reducing carbon fixation and biomass accumulation. Reproductive stages are especially vulnerable, with water deficit causing pollen sterility, poor anther dehiscence and reduced viability, ultimately compromising seed set. Prolonged drought further accelerates leaf senescence and restricts root growth, while osmotic imbalance and oxidative stress from reactive oxygen species (ROS) impair cellular metabolism and grain development. Given this multi-layered damage, no single fix can restore resilience. The primary goal, therefore, is to develop crop varieties that withstand extreme heat and severe drought without sacrificing yield potential and nutritional quality. Achieving this relies on an integrated framework that bridges classical field breeding with modern molecular biotechnology. Conventional methods such as selection, hybridization, mutational breeding and the untapped genetic diversity of landraces and wild relatives serve as the foundation for stress tolerance. Building on this foundation, genomic tools like QTL mapping, GWAS and genomic selection dissect complex polygenic stress traits, while marker-assisted selection (MAS) enables precise tracking and introgression of target alleles. Simultaneously, transgenic approaches and gene editing platforms like CRISPR-Cas9 allow direct, targeted sequence modifications, dramatically accelerating breeding cycles. Unifying these conventional, molecular, genomic and gene editing strategies empowers figures lies a cascade of physiological disruption. Water deficit triggers substantial yield losses, particularly during flowering breeders to engineer crops against climate-driven stresses, safeguarding long-term food security.

Breeding approaches

Conventional breeding for drought-tolerant crops relies on crossing parental lines to generate large segregating populations, from which promising individuals are selected based on desirable traits (Table 1). These selections undergo rigorous, multi-year field trials to evaluate their genetic performance across diverse environments. However, because this traditional approach relies almost entirely on phenotypes, it struggles to efficiently manage complex traits like drought resistance. The resulting heavy dependence on long-term testing and germplasm enhancement makes conventional breeding inherently slow and unable to keep pace with the urgent need for climate-resilient crops.

This reliance on narrow, phenotype-driven gene pools is precisely what pre-breeding sets out to correct. Pre-breeding bridges the gap between wild germplasm and modern elite crop varieties. Because elite gene pools often lack the genetic diversity needed to withstand severe abiotic stresses, pre-breeding focuses on identifying and transferring novel drought-tolerant genes and quantitative trait loci (QTLs) from wild relatives or unadapted donors. By introgressing these valuable traits into agronomically superior, adapted backgrounds, pre-breeding equips commercial breeding programs with the genetic variation necessary to develop robust, stress-tolerant crops and represented in the Table 2.

Table 1: Traits associated with drought tolerance tolerance (Kaur *et al.*, 2026)

Trait level	Key adaptive mechanisms	Main functional benefits	Specific examples/markers
Morphological	Root architecture modification	Maximizes water foraging	Increased root-to-shoot ratio
	Leaf area reduction	Minimizes transpiration	Early leaf senescence
	Dynamic leaf movement	Reduces light interception and heat load	Reversible leaf rolling or folding
	Altered biomass allocation	Optimizes resource use for survival.	Shortened life cycle
Physiological	Regulation of stomatal aperture	Immediate regulation of water vapour exit	ABA-mediated closure signals
	Turgor maintenance	Sustains growth during low water potential	Active osmotic adjustment
	Modulation of photosynthesis	Protects the photosynthetic apparatus	Non-photochemical quenching
	Stem/Leaf hydraulic conductivity	Prevents xylem cavitation and embolism	High Water Use Efficiency (WUE)
Biochemical	Biosynthesis of osmo-protectants	Stabilizes membranes and biomolecules.	Proline, Betaine, and Trehalose
	Antioxidant upregulation	Clears harmful oxidative molecules (ROS)	Enzymes like SOD, CAT, and APX
	Synthesis of stress-responsive proteins	Prevents protein denaturation	Synthesis of stress-responsive proteins: LEA and Heat Shock Proteins (HSPs)
	Metabolic reconfiguration	Shifts resources to stress-defence pathways	Increased phenolic compounds
Anatomical	Dermal barrier reinforcement	Forms a hydrophobic barrier to water loss	Thickened epicuticular wax/cuticle
	Stomatal architecture	Increases boundary layer resistance	Sunken stomata or dense trichomes
	Vascular structural change	Provides mechanical strength against collapse	Small, thick-walled xylem vessels
	Development of specialized tissues	Enhanced internal water storage/transport	Formation of aerenchyma or succulence

Table 2: Crop wild relatives for drought tolerance (Kapazoglou *et al.*, 2023)

Crops	Crop wild relatives
Rice	*Oryza australiensis, O. glaberrima, O. longistaminata, O. meridionalis, O. rufipogon, O. nivara, O. glumaepatula, O. grandiglumis*
Wheat	*Triticum dicoccoides, Aegilops tauschii*
Barley	*Hordeum vulgare spp. spontaneum*
Cotton	*G. tomentosum, G. herbaceum, G. darwinii*
Soybean	*G. soja, G. latifolia, G. canescens*
Groundnut	*Arachis Dardani, A. diogoi, A. duranensis, A. glabrata, A. magna*
Cowpea	*Vigna exilis, V. heterophylla, V kirkii, V. trilobata*

Molecular breeding holds a clear advantage over conventional breeding primarily because it operates directly at the genotype level using DNA markers, eliminating the sole reliance on visible traits. Conventional breeding is inherently time-consuming and heavily influenced by environmental variations, whereas molecular approaches allow for high-precision, environment-independent

selection at the early seedling stage, avoiding the need to raise crops to full maturity. Under drought stress, molecular techniques enhance the development of tolerant crops through three key strategies. The first is Marker-Assisted Backcrossing (MABC), which transfers major quantitative trait loci (QTLs) for traits like root architecture or reduced anthesis-silking interval into elite lines while minimizing linkage drag. Complementing this, Marker-Assisted Recurrent Selection (MARS), which intermates selected lines across multiple cycles to accumulate multiple minor-effect favourable alleles for complex traits like water-use efficiency. Extending beyond single-locus approaches, Genomic Selection (GS), which evaluates whole-genome marker profiles to calculate Genomic Estimated Breeding Values (GEBVs), bypassing single-QTL limitations and significantly accelerating selection cycles. To be successful, these approaches rely heavily on precise, high-throughput phenotyping alongside QTL mapping and candidate gene discovery. Through such candidate gene discovery efforts, several genes governing key drought-responsive pathways, spanning ABA signalling, osmotic regulation, ROS scavenging, and cuticular wax biosynthesis, have now been identified across major crop species (Table 3).

These identified genes are not merely catalogued, many have already been put to direct use through transgenic technology, which enables the introduction of drought-responsive genes across species barriers, complementing conventional breeding. A key target is the ABA signaling pathway, where SnRK2 kinases, released upon ABA perception, drive stomatal closure. Transgenic expression of DREB1A (from Arabidopsis thaliana, under the rd29A promoter) enhances water-use efficiency, with DREB1A-transformed groundnut showing deeper roots and improved pod yield under water deficit. NAC transcription factors are another major target: overexpression of the rice-native genes OsNAC6, OsNAC10, and OsNAC5 improves root architecture, drought tolerance, and grain yield in rice, while AtNAC2 (Arabidopsis thaliana) and MuNAC4 (horse gram, Macrotyloma uniflorum) confer similar benefits in their host species. The bZIP factor GBF3, native to Arabidopsis, confers combined drought and pathogen resistance, and miR169-mediated suppression of NF-YA factors, characterized in soybean (gma-miR169c) and validated in transgenic Arabidopsis and soybean hairy roots, adds post-transcriptional regulation. Beyond single-gene studies, these strategies have already translated into field-deployed products. Drought-tolerant maize (MON 87460) carries the cspB gene from the bacterium Bacillus subtilis, stabilizing proteins and photosynthetic structures to improve water-use efficiency, while transgenic rice expresses CSPB (also B. subtilis), Ubi1TPSP (a trehalose-6-phosphate synthase/phosphatase construct), and NHX1 (a vacuolar Na^+/H^+ antiporter, typically AtNHX1 from Arabidopsis) for field-level tolerance. LEA proteins such as HVA1 (from barley, Hordeum vulgare), aquaporins, and osmolyte-biosynthetic genes further protect against cellular dehydration, and gene-stacking, such as combined HVA1 (barley) and DREB (Arabidopsis-derived) expression in cotton, has achieved up to 30% higher lint yields under drought while maintaining fibre quality.

Table 3: Genes identified for drought tolerance in various crops (Wang *et al.*, 2021)

Functional category	**Protein function**	**Gene name**	**Species**
ABA receptor	PYR/ PYL/RCAR	*OsPYL9, TaPYL4*	*Oryza sativa, Triticum aestivum*
Protein kinase and protein phosphatase	CDPK	*GmCDPK3*	*Glycine max*
	CIPK	*OsCIPK*	*Oryza sativa*
	MAPK	*OsMPKK10.2*	*Oryza sativa*
	RLK	*GbRLK*	*Gossypium barbadense*
	SnRK	*TaSnRK2.9*	*Triticum aestivum*
	PP2C	*OsPP2C09, ZmPP2C-A*	*Oryza sativa, Zea mays*
Transcription factor and cofactor	AP2/ERF	*NtERF172*	*Nicotiana tabacum*
	bZIP	*GmbZIP1, TaAREB3*	*Glycine max, Triticum aestivum*
	HD-ZIP	*ZmOCL5*	*Zea mays*
	MYB	*OsMYB102*	*Oryza sativa*
	NAC	*TaNAC69, ZmNAC48*	*Triticum aestivum, Zea mays*
	Zinc finger	*OsDST*	*Oryza sativa*
	Transcription cofactor	*OsSKIPa, OsRIP18*	*Oryza sativa*
Metabolism	Abscisic acid metabolism	*OsDSM2, PvNCED1*	*Oryza sativa, Phaseolus vulgaris*
Osmotic regulation	Dehydrin	*SiDHN*	*Saussurea involucrata*
	Glycine betaine	*BADH*	*Spinacia oleracea*
	LEA	*OsLEA3-2*	*Oryza sativa*
	Mannitol	*mtlD*	*Eleusine coracana*
	Proline	*OsP5CS, OsOAT*	*Oryza sativa*
	Trehalose	*ZmT6P*	*Zea mays*
Protein turnover	E_3 ubiquitin ligase	*StRFP2, TaSDIR1*	*Solanum tuberosm, Triticum aestivum*
Protein modification	Farnesylation	*ERA1*	*Brassica napus*
	Sumoylation	*OsSIZ1*	*Oryza sativa*
ROS scavenging	Ascorbate peroxidase	*EcAPX1*	*Eleusine coracana*
	Similar to RCD One	*OsSRO1c*	*Oryza sativa*
	Superoxide dismutase	*SOD*	*Pisum sativum*
Transporters	Aquaporin	*MaPIP1;1, OsRWC3*	*Musa acuminata, Oryza sativa*
	Auxin efflux carrier	*OsPIN3t*	*Oryza sativa*
	Choline Dehydrogenase, V-H^+-PPase	*ZmbetA, ZmTsVP*	*Zea mays*

Functional category	Protein function	Gene name	Species
Cuticle wax	Vacuolar-type H^+ pyrophosphatase	*ZmVPP1*	*Zea mays*
	ABC transporter	*ZmGLOSSY13*	*Zea mays*
	Megaenzyme	*OsDWA1*	*Oryza sativa*
	Sterol desaturase	*OsGLOSSY1*	*Oryza sativa*

Table 4: Drought-tolerant crop varieties and hybrids

Crop	Varieties or hybrids
Rice	Sahbhagi Dhan, DRR Dhan 42, DRR Dhan 44, DRR Dhan 50, DRR Dhan 64 DRR Dhan 43, Swarna Shreya, CR Dhan 80, CR Dhan 802
Wheat	DBW 327, JKW 261, MP (JW) 1358
Maize	DHM 117, DHM 121, Birsa Makka-1
Pearl millet	RHB 177, RHB 273, GHB 1294, MPMH 42, GHB 538 improved
Finger millet	ML 365, Indira Ragi-1, ATL-1 (TNEc 1285)
Sorghum	CSV 17, CSV 18, CSH 19R, Phule Vasudha
Chickpea	JG 11, JG 16, RVG 201
Pigeon pea	ICPL 87119 (Asha), ICP 8863 (Maruti), PRG 176, Pusa 2001
Green gram	PDM 139, RMG 344, GM 4, VBN 4, VBN 8, IPM 02-3
Black gram	PU 31, VBN 6, VBN 8, TBG 104, TAU 1
Groundnut	Narayani, ICGV 91114, ICGV 03042, Kadiri 6, Kadiri 9
Mustard	Pusa Jai Kisan, Pusa Bold, NRCHB 101, RH 749
Sunflower	KBSH 53, KBSH 44, LSPH-35
Sugarcane	Co 86032, Co 85019, Co 94008, Co 99004, Co 2001-13

Conclusion

Climate-induced water stress now threatens global crop productivity, with documented yield losses across staple cereals and a severe burden on rainfed systems, which cover nearly 68% of India's net sown area. Drought triggers cascading physiological damage, from stomatal closure and impaired photosynthesis to reproductive failure, showing that no single intervention can deliver resilience alone. Conventional breeding remains foundational but is slowed by multi-year phenotypic evaluation, while pre-breeding and molecular tools like marker-assisted and genomic selection accelerate progress by unlocking wild diversity and enabling genotype-level selection. Transgenic and gene-editing platforms extend these gains through targeted genes such as DREB1A, NAC factors, and HVA1. Yet India invests barely 0.6-0.7% of agricultural GDP in R&D, against 2% or more in most developed nations, a gap that must close swiftly if drought-resilient genotypes are to reach the small and marginal farmers who form over 85% of the country's cultivators.

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